

Role of the soil invertebrates in determining the composition of soil microbial communities

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SUMMARY

1 The various mechanisms by which soil fauna can influence the composition of microbial communities are separated into three main categories: (i) comminution, channelling and mixing, (ii) grazing, (iii) dispersal, and discussed.

2 Comminution, channelling and mixing may reduce fungal species numbers and divert fungal successional patterns on decaying plant residues. This may be due to the sensitivity of various fungi to destruction of their thallus and microhabitat, thereby giving a competitive advantage to fast-growing, short life-cycle micro-organisms such as bacteria and *Mortierella* spp.

3 Grazing by the fauna on selected fungi may significantly alter fungal distribution and succession on decomposing leaf litter and may deleteriously affect plant growth by reducing the effectiveness of the mycorrhizal symbiosis. The impact of the fauna on their microbial food sources appears to be dependent on the grazing pressure of the invertebrate and possibly on the growth rate of the organism being grazed.

4 Many soil micro-organisms, particularly those commonly associated with the invertebrate body, may rely on the soil fauna for dispersal of their propagules. However, the success of the transmitted propagules in establishing themselves in new microhabitats requires further investigation. The interaction of the dispersal, grazing and comminution/mixing activities of the soil fauna in determining dynamic microbial communities is speculated upon.

INTRODUCTION

Despite the low estimated contribution of soil fauna to total soil respiratory metabolism in comparison with the soil microflora (Reichle 1977; Persson *et al.* 1980), the density of various faunal groups can be very high (Petersen & Luxton 1982). Therefore, it has been speculated that the roles of the soil fauna may be more subtle than is evident from their contributions to total soil metabolic activity. These roles include the regulation of decomposition and mineral cycling processes and direct and indirect effects on soil microbial activities (Seastedt 1984).

The efficiency of the soil microflora in decomposing organic debris is determined by resource quality and quantity, and by both the inoculum potential, and the competitive ability of the decomposer organisms (Garrett 1970). By altering resource quality and influencing inoculum potential and competitive saprophytic

ability of decomposers and root-infecting fungi, soil/litter invertebrates can affect microbial community structure as well as decomposition/mineralization processes.

The type of influence of soil fauna on the microflora will depend largely on the animal's size and its method of feeding. Generally, a direct relationship exists between animal size and the size of ingested food particles. Therefore, it seems likely that smaller animals have a high chance of feeding on specific components of the microflora. Based on their size, numbers, mobility, and wide diversity of feeding strategies (Burgess & Raw 1967; Wallwork 1970; Petersen & Luxton 1982), the activities of the soil fauna in relation to their potential influence on soil micro-organisms can be separated into three main categories:

- (i) comminution, mixing and channelling of litter and soil;
- (ii) grazing on the microflora;
- (iii) dispersal of microbial propagules.

Information regarding the specific roles of the macro-, meso-, and microfauna in structuring microbial communities is sparse and has been generated from studies conducted in a wide variety of systems including litter/soil microcosms, cattle and rabbit dung, and woodland streams. An attempt is made here to review these studies within the context of the three categories of faunal activities mentioned previously. Since much of the data has been obtained from laboratory studies, extrapolation to field conditions entails much speculation

COMMINUTION, CHANNELLING AND MIXING

In the present context comminution is defined as the fragmentation and mastication of plant debris including the microflora growing within the plant residues. In contrast, grazing implies that the invertebrate has a feeding mechanism which allows separation of the microflora from its food base, with little destruction to the microbial food base.

It has been suggested that fragmentation of organic matter, channelling, and mixing of soil components are key roles by which soil fauna stimulate microbial activity, thereby enhancing the rate of organic matter decomposition (Kevan 1962; Wallwork 1970; Crossley 1977; Swift, Heal & Anderson 1979). Both uningested litter fragments and ingested (later defaecated) materials result from faunal comminution activities. The size of the uningested fragments will presumably be larger than the size of the ingested fragments where the degree of reduction will depend on the size of the invertebrate. For example, plant debris is reduced to particles 200–300 μm diameter by earthworms and millipedes, 100–200 μm by medium-sized arthropods and 20–50 μm by micro-arthropods (Swift *et al.* 1979). This consumed material is expelled as faeces, with the constituent particle size varying with different faunal groups; a factor which may also determine the persistence of the faeces (Webb 1977). The pelletization of organic debris, and resultant effects through changed pore volume, on moisture retention and aeration, will alter the balance between bacteria and fungi. Maximal bacterial development has been recorded in fine textured soils (Bhaumik & Clark 1947), and Parr, Parkinson &

Norman (1967) showed bacterial respiration to be greatest in artificial systems with small pore size, whereas fungal vegetative activity (*Trichoderma viride*) was greatest in systems of large pore size. The importance of pore size in allowing fungal sporulation has been shown for *Cunninghamella*, *Botrytis*, *Rhizopus* and *Mucor* by Kubišna (1938) and for *Curvularis* and *Pythium* by Griffin (1963a, b). The movement of fungal spores under changes in moisture tension is also limited by the size of the pores in soil and by spore size (Dickinson & Parkinson 1970) and limitations of space may be of considerable importance for the development of sequential microbial populations on organic substrata (Stotzky & Norman 1961).

Extrapolating these data to sites of faecal accumulation (e.g. F₂ and H layers of forest soils) it might be expected that in macro-arthropod faeces the constituent particles would be large enough to allow fungal growth and sporulation, whereas the compaction of particles in micro-arthropod pellets would only allow bacterial growth. Support for this extrapolation has been given by Hanlon (1981b).

In comparison with undigested resources where no alteration of chemical quality would occur, increased NH₄-N levels (Parle 1963b; Bocock 1963; Anderson, Ineson & Huish 1983), pH (Hanlon 1981c), and carbohydrate levels (Parle 1963b) have been observed in millipede faeces and earthworm casts. A higher bacterial biomass has been recorded from invertebrate faeces than from uningested food materials (Parle 1963a; Reyes & Tiedje 1975; Brown, Swift & Mitchell 1978; Anderson & Bignell 1980, Hanlon 1981c) and this may be attributed to altered chemical quality of the faeces or to bacterial multiplication within the invertebrate gut (Parle 1963a; Anderson & Bignell 1980; Hanlon 1981c).

Fungi appear to be susceptible to damage as a result of the comminution and digestion process (Hanlon 1981b), this possibly being related to the size of the animal involved. Thus, fungal viability may be less affected after passage through millipede and earthworm guts (as indicated by the fungal isolation data of Nicholson, Bocock & Heal 1966; Parle 1963b) than after passage through guts of *Collembola* (Ponge & Charpentier 1981). It appears that the main effect of macro-invertebrate feeding (and resource comminution) is to stimulate bacterial activity and reduce fungal biomass, an effect exemplified in the microcosm study of Hanlon & Anderson (1980) and the dung study of Lussenhop *et al.* (1980).

Moisture conditions and their variations at faunal feeding times may influence the subsequent microbial colonization of casts and faeces. Wet conditions may give an advantage to bacteria, which may decrease as the food base dries (Nicholson, Bocock & Heal 1966). Alternating wet and dry conditions may favour fungal activity.

There have been very few studies regarding the effects of resource comminution on the specific nature of the microflora. In a laboratory study, Wicklow & Yocum (1982) recorded a reduction in the number of coprophilous fungal species in rabbit dung with increased density of dipteran larvae (Table 1). It was suggested that the decrease was due to damage to the mycelial thallus, with some fungi (*Podospora tetraspora*, *Lasiobolus intermedius*) being more sensitive than others. The feeding behaviour of the larvae consisted of both channelling within the dung pellets and

TABLE 1. Dipteran larvae density effects on the number of species within coprophilous fungal communities (from Wicklow & Yocum 1982)

	Initial larval density per dung sample							
	0	5	10	25	50	70	100	125
Total fungal species	14	14	12	8	9	6	9	7
Mean species per 2 g sample	6	6	5.2	5.2	5.2	3.0	3.2	3.2

grazing on the pellet surface which, in contrast to selective grazing on a particular component of the microflora, was thought to have caused the reduction in fungal species. This study emphasizes the importance of distinguishing between comminution/channelling activities and selective grazing since these two feeding behaviours may influence microbial communities in completely different ways.

In another study, Lussenhop *et al.* (1980) observed that arthropods added to cattle dung in the field had no significant effect on numbers of fungal species which fruited although hyphal density was reduced. Unlike conditions in the laboratory, where moisture levels of experimental material can be controlled, dung in the field eventually dries out, resulting in emigration and pupation of insects. Thus, climatic properties were believed to exert a major influence on invertebrate-microfloral interactions. The inconsistency of results obtained in the laboratory and the field may be largely due to the interactions of abiotic variables with insect and microbial life cycles. These interactions should be taken into account when designing laboratory microcosm experiments intended to elucidate field observations.

In addition to potentially altering microbial community structure by affecting fungal species abundance and richness, the comminutive activities of the soil fauna may also affect fungal successional patterns on decaying plant debris. The mechanisms of replacement involved in fungal successions have been thoroughly reviewed by Frankland (1981) and summed up by her as follows 'a decomposer can replace another species when changes in the substrate (or site) have interacted with changes in its relative competitive saprophytic ability and inoculum potential giving it a decisive advantage.' By altering substrate quality and a colonizer's inoculum potential, soil invertebrates may have a controlling influence on successional patterns. For example, Swift (1982) observed that when decomposing branchwood was invaded by dipteran larvae, the Basidiomycete community colonizing the wood was largely replaced by fungi typical of the soil microflora such as moniliaceous and mucoraceous forms. The sensitivity of the Basidiomycete biomass to comminution and mixing thereby reducing its inoculum potential was believed to be one of the factors causing the shift in fungi—a factor also considered by Wicklow & Yocum (1982) for coprophilous fungi in rabbit dung. Other factors included a change in the physical structure of the resource as a consequence of invertebrate activity and the transport of microbial propagules from the litter and soil into the wood via Collembola and mites.

Fungal successional sequences on leaf litter may also be diverted as a result of passage of microbially colonized litter through the invertebrate gut. Nicholson, Bockock & Heal (1966) found that when faeces of millipedes previously fed on 6–12

TABLE 2. Frequently-isolated fungi from ingested, defaecated hazel leaves and uningested hazel leaves in the field (from Nicholson, Bockock & Heal 1966; Hering 1965)

Fungi isolated	Age of ingested matter in faeces (mo)			Age of uningested organic matter (mo)		
	12	14	18	12	14	18
<i>Cladosporium herbarum</i>	+	+	-	+	+	+
<i>Geomyces cretaceus</i>	+	+	+	-	-	-
<i>Mucor hiemalis</i>	+	+	-	+	+	-
<i>M. ramannianus</i>	+	-	-	+	+	+
<i>Mortierella isabellina</i>	+	+	-	-	-	-
<i>Trichoderma sporulosum</i>	-	+	+	-	-	-
<i>Phoma</i> sp.	-	+	+	-	-	-
<i>Paecilomyces farinosus</i>	-	-	-	+	+	+
<i>Aureobasidium pullulans</i>	-	-	-	+	+	+
<i>Penicillium frequentans</i>	-	-	-	+	+	-
<i>P. thomii</i>	-	-	-	+	+	+
<i>Trichoderma viride</i>	-	-	-	-	+	+

month old hazel litter were placed in the field, they were initially colonized by Phycomycetes such as *Mortierella* and *Mucor* (fungi capable of rapid exploitation of easily assimilable materials), followed by Ascomycetes and Fungi Imperfecti such as *Phoma* and *Trichoderma sporulosum* (Table 2). This successional pattern did not correspond with the pattern of fungal colonization observed on decaying, uningested hazel leaves (Hering 1965) (Table 2), but was thought to resemble more closely that found on dung.

As is the case for ingested plant debris, the size of the uningested particles will depend to a large extent on the size of the animal concerned. The exposure of uncolonized tissues in uningested leaf fragments will provide new surfaces for microbial colonization and may also result in the development of more continuous water films thereby promoting bacterial colonization (Griffin 1969). The decay of uningested fragments may be stimulated if they are withdrawn into earthworm burrows where environmental conditions are more conducive to microbial growth and organic matter decomposition. Burrowing in soil, mining in plant tissues, and channelling of wood may result in greater aeration which stimulates fungal growth and sporulation (Kubiena 1938; Warcup 1965; Griffin 1969), although Swift (1981) suggested that comminution of wood could also lead to higher moisture contents causing a drop in oxygen levels and a subsequent inhibition of Basidiomycete growth.

In aquatic systems, where leaf-eating invertebrates selectively feed on parts of leaves heavily colonized by micro-organisms, Bärlocher (1980) observed that invertebrate feeding on oak and larch leaves reduced fungal species number. He hypothesized that this was due to the removal of portions of leaf which, if they had not been consumed, would be available for colonization by later successional species, i.e. invertebrate consumption of both the resource and the microbes colonizing this resource, deleted the late successional phase and prolonged the persis-

tence of early successional species. No equivalent studies have been done in terrestrial ecosystems, but study is required to determine if the fungal successional pattern on rejected plant debris (e.g. lignified materials) is altered as a result of selective consumption of micro-organisms associated with the more palatable plant material

GRAZING

Grazing, as defined earlier, is the selective removal of microbial tissue from its resource by members of the microfauna (protozoa, nematodes) and mesofauna (enchytraeids, Collembola, mites, dipteran larvae) without extensive destruction of the resource. There is much documentation of exploitation of microbial biomass by these members of the soil fauna as a result of gut content analyses and feeding preference studies under laboratory conditions. The present discussion will deal mainly with data collected for organisms in temperate woodlands.

Microbial food sources of microfauna

Bacteria and yeasts are major food sources for protozoa in soil (Stout & Heal 1967; Stout 1974), and laboratory studies have shown preferential feeding by these organisms (Stout & Heal 1967) for members of the Pseudomonadaceae and Enterobacteriaceae, and yeasts such as *Rhodotorula*, *Saccharomyces* and *Kloeckera*. Some bacteria, actinomycetes (*Streptomyces griseus*) and fungi (*Trichoderma viride*) produce extracellular substances toxic to protozoa. Because protozoa generally prefer fast-growing, zymogenous micro-organisms, Stout (1974) suggested that they would flourish in habitats such as the rhizosphere where such micro-organisms would be stimulated by root exudates. In the soil, where a mainly autochthonous microflora was believed to predominate, micropredation could influence the composition of the bacterial flora (Stout 1974). Research is necessary to support these statements.

Nematodes use 'protoplasm' as their major food (Overgaard Nielsen 1967) and obtain this from a variety of sources including bacteria and fungi by applying a range of feeding mechanisms. There is little evidence of preferential feeding by bacterivorous nematodes but their growth rates may vary with different bacteria (Twinn 1974). Mycophagous nematodes feed on many root-inhabiting fungi (Riffle 1971) including vesicular-arbuscular mycorrhizal fungi (Salawu & Estey 1979), endomycorrhizal fungi of Ericaceae (Shafer, Rhodes & Riedel 1981) and ectomycorrhizal fungi (Sutherland & Fortin 1968; Riffle 1967, 1971).

Microbial food sources of mesofauna

Gut content analyses of field-collected mites and Collembola have shown the majority of animals to be non-specific feeders (Harding & Stuttard 1974; Anderson & Healey 1972; Anderson 1975; Behan-Pelletier & Hill 1983; Takeda & Ichimura

1983) with some mite species appearing to be either predominantly or exclusively mycophagous (Anderson & Healey 1972; Behan-Pelletier & Hill 1983). However, many of the micro-arthropods classified as panphytophages (Luxton 1972) have been observed to be mainly mycophagous (Poole 1959; Hågvar & Kjondal 1981; Mitchell & Parkinson 1976). Factors such as animal size (Anderson 1975) and availability of food items in particular microhabitats (Wallwork 1970; Petersen 1971) may influence the amount of fungus material consumed.

In contrast to the data from gut content analyses, laboratory experiments have generally shown not only preferential feeding by mites and Collembola on fungi but also their capability for selecting specific fungal species (e.g. Hartenstein 1962; Mills & Sinha 1971; McMillan 1976; Mitchell & Parkinson 1976; Visser & Whitaker 1977; Addison & Parkinson 1978). While the relevance of these studies to field situations may be questioned, they do not allow clarification of possible microflora-fauna relationship in the field. The relevance of this type of study is enhanced if the test organisms have the potential of interacting in the field. Newell (1984a) showed that *Onychiurus latus*, a common mycophagous Collembola at her field site, preferred mycelium of *Marasmius androsaceus* to that of *Mycena galopus*, not only in laboratory experiments but also in field tests.

Enchytraeids and dipteran larvae have been shown to accelerate organic matter decay rates (Standen 1978) and this may be related to their selective grazing on fungi (Dash & Cragg 1972). Many dipteran species are associated with fungal fruit bodies (Buxton 1960) but studies of their influence on fungal growth and development have concentrated on their effects on cultivated mushrooms (Binns 1980).

Boddy, Coates & Rayner (1983) reported that a volatile material, produced in zones of intraspecific antagonism between certain wood-decaying Basidiomycotina and Ascomycotina, was attractive to Mycetophilid fungus gnats. They suggested that this could significantly increase the consequences of grazing if it occurred in the field.

Effects of grazing in structuring microbial communities

If selective animal grazing on specific groups of the microflora occurs it could have a significant influence on microbial community structure. This influence, both in soil/litter systems and on roots will depend on: (i) grazing pressure, which is dependent on the density of grazers, the growth and turnover rates of the grazer and the time spent by the grazer on its food sources; (ii) growth rate, nutritional quality and physiological condition of the grazed organism which will determine its competitive ability; (iii) the ability of the food source to escape grazing, for example, by the production of toxic secondary metabolites.

Selective grazing by protozoa may alter the population density of specific bacteria (Habte & Alexander 1975). Given the potential high growth and turnover rates of protozoa and nematodes, their impact on the soil microflora, particularly the impact of nematodes on slow growing fungi, could be considerable.

Laboratory studies have shown that the effect of collembolan grazing on senes-

cent fungi can be dependent on the nutritional quality of the fungal food base, with fungi grown under low nutrient regimes exhibiting a reduction in activity in the presence of Collembola and fungi grown on nutrient rich substrates being stimulated by faunal grazing (Hanlon 1981a). Under conditions of high grazing pressure it appears that bacteria have a competitive advantage over fungi (Hanlon & Anderson 1979); however, the environmental conditions used (e.g. moisture), the time course of the study and the potential role of Collembola as dispersal agents of bacteria could give the bacteria a competitive advantage regardless of direct grazing by Collembola on the fungus.

Destruction of fungal thalli through grazing may alter not only the balance between bacteria and fungi but, if selective destruction occurs, also the dynamics of fungal colonization of both decaying leaf litter and roots. Thus, in a microcosm study, selective fungal feeding by Collembola in *Populus tremuloides* leaf litter effectively reduced the competitive colonizing ability of a preferred fungus (sterile dark form), giving a less preferred fungus (Basidiomycete) the competitive advantage (Parkinson, Visser & Whittaker 1979). In this way fungal succession appeared to be advanced and the impact of this in increasing litter decay rate was considered likely since the basidiomycete had an active cellulolytic potential not exhibited by the sterile dark form.

Laboratory and field studies performed by Newell (1984b) have demonstrated the effects of selective grazing by Collembola on competitive saprophytic colonization of Sitka spruce needles by two common litter-decaying Basidiomycetes, *Marasmius androsaceus* and *Mycena galopus*. Selective grazing on *M. androsaceus* (the fungus with higher colonizing ability) gave *M. galopus* a competitive advantage. Exclusion experiments in the field indicated an inverse relationship between collembolan density and the activity of the preferred fungus. Depending on the fungal species, collembolan grazing either stimulated litter decomposition (*M. androsaceus*) or reduced litter decay (*M. galopus*). Possibly, *M. androsaceus* is less sensitive than *M. galopus* to a reduction in biomass resulting from grazing because the former has a faster growth rate.

Invertebrate grazing on root region microfloras may have significant consequences on both the micro-organisms and plant growth. Selective grazing by the mycophagous nematode, *Aphelenchus avenae*, prevented the establishment of the mycorrhizal relationship between *Pinus resinosa* and *Suillus granulatus*; however, plant growth was not significantly reduced (Sutherland & Fortin 1968). In a study by Warnock, Fitter & Usher (1982) it was observed that the rate of growth of the vesicular-arbuscular mycorrhizal fungus, *Glomus fasciculatum*, within pre-infected leek roots was not substantially reduced by the presence of the Collembola, *Folsomia candida*. However, plant growth of both mycorrhizal and nonmycorrhizal leeks was adversely affected by the activities of *F. candida* with the effect being more pronounced for mycorrhizal plants. It was believed that the reduction in growth of the mycorrhizal plants was the result of *F. candida* feeding on the extramatrical hyphae of the fungus, thereby negating the beneficial effects usually conferred upon the host by the fungus. The observations made in this study suggest

that the influence of the soil fauna on the microflora may be very subtle and illustrate how little we understand the potential impact of grazers on microbial processes in the below-ground system.

Collembolan grazing may reduce the effectiveness of root pathogens or alter the species composition of the root region microflora thereby affecting interactions with symbionts (Wiggins & Curl 1979). Root exudates are a source of easily assimilable carbon compounds which if not immobilized by mycorrhizal fungi, will presumably stimulate the non-symbiotic root region microflora. This in turn could cause an increase in invertebrates feeding on the microflora (Clarholm 1981). More attention is required on the impact of grazers on root region microfloras in the presence and absence of mycorrhizal fungi.

The litter-soil-plant root system comprises a complex mosaic of microsites for microbial development, superimposed on which are aggregations of soil invertebrates. Hence, consideration of the mechanism by which soil fauna may alter fungal community structure is very difficult, particularly when substantive data are very scarce. In view of this, it may be instructive to consider the possible implications of other plant-herbivore systems to trophic interactions in soil.

In a study of protected intertidal communities, Lubchenco (1983) showed that preferential grazing by periwinkle snails on early successional ephemeral algae allowed an accelerated establishment of later successional algal species, by removing the inhibition caused by the rapid growth and reproductive rate of the ephemerals. A similar situation may occur during fungal colonization of leaf debris or plant roots, although here the successional sequences are complicated by micro-environmental and resource quality factors which cause much instability during early successional phases. Nevertheless, preferential faunal grazing on early successional fungi, e.g. *Cladosporium* spp. on leaf litter or *Thelephora terrestris* on pine roots, could allow accelerated fungal succession on these resources.

It was also observed in intertidal communities that the grazers not only preferred early ephemeral species but avoided consuming the later successional algal species, possibly because the algae contained higher levels of polyphenolic compounds. The production of secondary metabolites by some fungi, particularly Basidiomycetes, may serve the same purpose. Sutherland & Fortin (1968) found that *Rhizopogon luteolus*, an ectomycorrhizal fungus, was toxic to nematodes, an effect which may be due to the production of calcium oxalate by this fungus (Malajczuk & Cromack 1982). Binns (1980) considered that calcium oxalate limited feeding on mycelium of *Agaricus bisporus* by sciarid larvae and caused subsequent migration of the adults. In the same way, Richter (1980) observed that slugs, fed on immature *Amanita muscaria* died and suggested that toxic alkaloids, similar to those known to deter invertebrate herbivory of higher plants, could be responsible. Many slow growing Basidiomycetes which generally predominate late in the successional sequence, and for which destruction of the thallus could significantly reduce their competitive abilities and opportunities to reproduce, may deter grazing by producing toxic substances.

In addition to the production of toxic metabolites by older plants, Lubchenco

(1983) observed that, in the case of young plants which were susceptible to grazing, the heterogeneity of the substratum, plant density and patchy grazing behaviour of the herbivore were important factors in the successful establishment of later successional algae. In the below-ground system an increase in heterogeneity of microhabitats due to a reduction in litter particle size (with attendant decrease in pore size) and the penetration of roots or plant debris by fungal hyphae could provide a mechanism by which young colonies and actively growing hyphal tips of later successional fungi are protected from faunal grazing. Patchy grazing may not only allow the escape of some fungal species, but could significantly stimulate their activity (presumably by release of nutrients) as demonstrated by Bengtsson & Rundgren (1983). Consequently, preferential invertebrate grazing on early successional fungi, because later successional species have evolved strategies to deter grazing, could result in accelerated fungal succession.

The role of faunal grazers in regulating fungal species diversity in litter-soil systems or on roots has not been investigated. Lubchenco (1978) concluded that the impact of an unspecialized grazer on the species diversity of its food source depended on grazing intensities and on the food preferences of the grazer, coupled with the competitive relationships between the food plants. The effect of faunal grazing on fungal species diversity may also be controlled by these factors.

There are various special cases of invertebrates causing local changes in fungal community structure in soil. A number of arthropods secrete volatile fungistatic and fungicidal materials (Roth 1961). *Scaptocoris divergens*, a soil-burrowing hemipteran, produces substances which are fungistatic or fungicidal to some soil-borne pathogenic fungi and several soil saprophytes (Timonin 1961).

The mutualistic association between some ant species and fungi sometimes results in extensive fungus gardens where a dominant single fungus is selectively maintained even though it is exposed to potentially high contamination. The supplying of suitable food resources, 'weeding', and the production of substances inhibitory to saprophytic bacteria and fungi (Weber 1972; Schildknecht & Koob 1971) by the ants are the methods by which the dominance of one species of fungus is maintained.

DISPERSAL

In addition to their roles in comminuting plant debris and grazing, soil invertebrates have also been considered important as dispersal agents of microbial inoculum.

Although the Phallales have been considered to be the only group of fungi which have evolved total dependence on insects for spore dispersal (Ingold 1971), there are a number of cases where fungi have developed specialized relationships to ensure insect dispersal of their spores (e.g. various rusts and smuts, *Ceratocystis ulmi*, *Stereum sanguinolentum*). However, all these cases involve the dispersal of spores between resources above-ground, where wind and water are considered the major dispersal mechanisms. Below-ground, members of the soil fauna may well be primary agents of spore transport. This would apply particularly in dry climates

here propagule transport via water percolation through the profile would be expected to be minimal.

The spread of microbial inoculum may occur by means of propagules carried on external parts of the fauna and by inoculum passed through the gut and expelled as faeces (provided viability of this inoculum is maintained). Jacot (1930) observed fungal spores attached to the exterior of various Phthiracarid mite species, and similar observations have been made for a range of mite and Collembola species by Vitkamp (1960), Warcup (1965) and others.

MacNamara in 1924 observed fungal spores in the guts of mandibulate Collembola, and since then numerous investigators have commented on the presence of fungal spores and hyphal fragments in the guts and faeces of the soil mites, Collembola and enchytraeids. The probable importance of fungal spores as a major component of the diet of these soil animals has prompted researchers to quantify the faecal component of gut contents (Poole 1959; Gilmore & Raffensperger 1970; Anderson 1975, 1978; Behan-Pelletier & Hill 1983). Laboratory experiments on food preferences have suggested that some Collembola species prefer feeding on fungal spores, depending on spore type, rather than on hyphae (Knight & Angel 1967; McMillan 1976).

Much of the work on the role of soil animals as dispersal agents of fungi in litter-soil systems has emphasized the qualitative nature of the fungi associated with the animals or in their faecal pellets. Talbot (1952) recorded many species of fungi associated with wood (including Basidiomycetes) in the guts of woodlice, mites, springtails and slugs. Viability tests of spores of the wood decay fungus, *Merulius lacrymans*, after passage through woodlice guts suggested that there was a reduction in spore viability after digestion, and that the spores which retained viability required a longer time to germinate than uningested spores. It was postulated that insect activity was a major spore dispersal mechanism for some resupinate Hymenomycetes.

The majority of studies done to date indicate that mites and Collembola extracted from a range of habitats have associated with them approximately twenty species of fungi (Christen 1975; Behan & Hill 1978; Pherson & Beattie 1979). These species are comprised mainly of heavily sporulating forms including soil saprophytes (*Mortierella*, *Cladosporium*, *Penicillium*, *Chrysosporium*, *Aspergillus*), potential invertebrate parasites (*Beauveria*, *Paecilomyces*), and potential plant pathogens (*Fusarium*). They have the ability to metabolize a wide variety of substrates (Behan & Hill 1978) and generally reflect the most common genera isolated from the material from which the animals were extracted (Pherson & Beattie, 1979). The number of fungal genera associated with each animal appears to be related to body surface area, with the Collembola and Acari having fewer generally per individual (0.5) than the Coleoptera and Oligochaeta (1–2) (Pherson & Beattie 1979).

S. Visser, M. Hassall & D. Parkinson (unpubl.) examined the fungal taxa associated with the Collembolan, *Onychiurus subtenuis*, extracted from the L, F₁, F₂, and H layers of an aspen woodland. Individual animals (105 per layer) were placed on

TABLE 3. Numbers of fungal propagules and taxa associated with *O. subtenius* extracted from the L, F₁, F₂, and H layers of an aspen poplar woodland. Values are ranges of arithmetic means for thirty-five animals from each of three cores

	Litter layer			
	L	F ₁	F ₂	H
Number of propagules	3.1–5.5	2.4–5.0	2.5–5.0	2.5–3.1
Number of taxa	2.8–3.8	1.8–2.9	1.8–2.4	1.9–2.1

2% malt extract agar (with and without addition of bactericidal antibiotics), allowed to wander over the plates for 24 hours and then squashed into the medium to ensure that microbial propagules from exterior and interior body parts could be recorded. Bacteria and fungi were isolated from the tracks and bodies of all individuals, with the greatest number of fungal propagules and taxa being obtained from animals from the L layer and lowest from those from the H layer (Table 3). A total of 120 taxa of fungi were isolated (Table 4), with the most frequently occurring species (*Beauveria bassiana*, *Cladosporium cladosporioides*, *C. herbarum*, *Mortierella alpina*, *M. elongata* and *Penicillium raistrickii*) being similar to those isolated by previous investigators. This group of fungi was isolated from animals extracted from all layers; however, some species showed increasing or decreasing

TABLE 4. The percentage of occurrence (\pm SD) of the most common species isolated from the tracks and body of *O. subtenius*

	Litter layer			
Fungal species	L	F ₁	F ₂	H
<i>Beauveria bassiana</i> (Bals.) Vuill.	11 ^a (13)	62 ^a (64)	51 ^a (58)	5 ^a (6)
<i>Cladosporium cladosporioides</i> (Fres.) de Vries	124 ^d (53)	38 ^c (21)	15 ^b (3)	4 ^a (2)
<i>C. herbarum</i> (Pers.) Link ex Gray	42 ^a (4)	19 ^a (10)	13 ^a (2)	34 ^a (27)
<i>Mortierella alpina</i> Peyronel	34 ^a (10)	79 ^a (19)	142 ^b (17)	144 ^b (28)
<i>M. elongata</i> Linnem.	5 ^a (3)	19 ^a (16)	11 ^a (13)	25 ^a (4)
<i>M. exigua</i> Linnem.	4 (3)	3 (0)	1 (2)	2 (3)
<i>Penicillium raistrickii</i> Smith	27 ^b (12)	24 ^b (8)	68 ^b (70)	1 ^a (2)
<i>Penicillium</i> spp. (14 forms)	12 (4)	12 (7)	14 (7)	11 (13)
<i>Verticillium leptobactrum</i> W. Gams	8 ^a (3)	9 ^a (6)	9 ^a (7)	4 ^a (4)
<i>V. psalliotae</i> Treschow	6 ^a (3)	1 ^a (2)	8 ^a (7)	5 ^a (4)
Sterile dark (9 forms)	21 (29)	9 (3)	2 (3)	11 (3)
Sterile hyaline (24 forms)	28 (9)	20 (13)	8 (2)	6 (3)
<i>Acremonium strictum</i> W. Gams	4 (3)	2 (3)	1 (2)	0
<i>Phoma eupyrena</i> Sacc.	11 (13)	3 (5)	1 (2)	0
<i>Calcarisporium arbuscula</i> Preuss	9 (4)	19 (18)	0	0
<i>Coleophoma cylindrospora</i> (Desm.) Hohn.	12 (12)	3 (5)	0	0
<i>Phialophora</i> sp. KS 88	1 (2)	11 (11)	0	0
<i>Eleutheromyces subulatus</i> (Fr.) Fckl.	17 (30)	0	0	0
Total species and forms isolated/layer	45	35	24	27

Values are means of the number of occurrences for each species/35 animals \times 100. Where possible data analysed by one-way ANOVA with blocking. Values in each row followed by the same letter do not differ significantly ($P < 0.05$).

frequency of occurrence with depth, e.g. the occurrence of *C. cladosporioides* on Collembola from the L layer was significantly greater than on animals from the H layer, while the reverse was true for the occurrence of *M. alpina*. Many fungal taxa were restricted to animals extracted from one or two litter layers, and included not only sporulating species but also slow-growing non-sporulating dark and hyaline forms. No clamped Basidiomycete forms were isolated. Generally the pattern of fungal occurrences on *O. subtenuis* was similar to that previously recorded on L, F₁, F₂ and H layer organic material (Visser & Parkinson 1975). Two exceptions were *Beauveria bassiana* and *Trichoderma* spp. The former, an insect parasite, was common on the animals extracted from the F₁ layer (62% frequency of occurrence) but much less frequent in the F₁ layer itself (7% frequency of occurrence), while the latter were predominant in the H layer material (71% frequency of occurrence), but never isolated from the animals extracted from the H layer. Some species of *Trichoderma* have been shown to be antagonistic to such soil invertebrates as nematodes (Miller & Anagnostakis (1977) and hence may also be toxic to *O. subtenuis*. From this study it was concluded that *O. subtenuis* was capable of dispersing a wide variety of fungi throughout the LFH layers of the organic horizon.

Since faecal pellets are often assumed to be major sources of fungal inoculum, pellets from *O. subtenuis* extracted from each litter layer were plated on nutrient agar. Approximately 50% of these pellets yielded fungi. Van der Drift (1965) reported that, after feeding *Onychiurus quadricellatus* on a sporulating colony of *Cladosporium* sp., hyphae in the pellets were non-viable and only 13% of the visually undamaged spores germinated compared with 83% germination for uningested spores. Ponge & Charpentier (1981) reported significant reductions in spore viability of a range of soil and litter fungi as a result of gut passage through Collembola. Digestion resulted in the disappearance of spore protoplasm and caused a considerable degree of physical damage to large-sized spores such as those of *Ulocladium consortiale*. Thus, it appears that faecal pellets, particularly those of micro-arthropods, may not be as important fungal dispersal agents as is transport via exterior body parts. Macro-invertebrates may cause less damage to fungal propagules, and therefore their faeces may exhibit greater fungal viability. For example, viable spores of the Endogonaceae have been reported from earthworm casts, leading to the suggestion that earthworm activity could have a significant impact on the distribution of vesicular-arbuscular mycorrhizal fungi within the soil profile (McIlveen & Cole 1976).

Although a wide variety of micro-organisms have been found associated with soil-dwelling invertebrates, evidence that the associated organisms become established in habitats different from those where the propagules were gathered is only available from sterile systems. Earthworms were observed to increase significantly the rate of spread of *Cephalosporium*, *Trichoderma viride*, *Rhizopus nigricans* and *Penicillium spinulosum* in autoclaved garden soil (Hutchinson & Kamel 1956), and Witkamp (1960) found that growth of fungal mycelium from unsterilized forest soil into sterilized forest soil was stimulated by the activities of oribatid mites. Bacteria

are particularly successful after introduction of their faunal carriers into sterilized and inoculated litter systems (Parkinson, Visser & Whittaker 1979).

The dissemination and establishment of fungi and bacteria by Collembola into the rhizosphere of cotton plants growing in sterilized soil has also been shown (Wiggins & Curl 1979). *Aspergillus flavus*, *Trichoderma harzianum*, *Fusarium oxysporum* f. sp. *vasinfectum* readily colonized rhizosphere soil and root tissue after the introduction of Collembola reared on these particular organisms. Bacteria were readily transported into aseptic systems to which field-collected Collembola were introduced.

Soil-dwelling invertebrates are often found associated with the fruit-bodies of ectomycorrhizal fungi; however, their importance in the dissemination of mycorrhizal propagules and the establishment of the transported fungi on susceptible host roots has not been determined.

DISPERSAL AND MICROBIAL COMMUNITY STRUCTURE

The establishment of the transported propagules in non-sterile conditions requires that the propagules must germinate, colonize and exploit a resource in the presence of competition from the indigenous microflora. Therefore, before an organism can successfully colonize a substrate which it has the metabolic potential to exploit, its inoculum potential and competitive saprophytic ability must be high enough to overcome this competition unless these same features of the indigenous micro-organisms are reduced by faunal activity or by adverse microclimatic conditions. Through their comminution and grazing activities, fauna may not only reduce competition from micro-organisms they graze upon, but may at the same time provide uncolonized microhabitats for colonization by propagules carried on their body.

Many of the organisms frequently associated with soil invertebrates have the capacity to grow rapidly and sporulate profusely. This group of organisms, consisting of the bacteria and such fungi as *Penicillium* spp., *Cladosporium* spp., *Mortierella* spp. and *Trichoderma* spp., exhibit characteristics which resemble those of an opportunist or *r*-selected group of organisms (Pianka 1970). It is possible that these micro-organisms are dependent to a large degree on the soil fauna for their persistence in the litter-soil-root system. The fauna not only provide them with transport, but also with new areas and substrates for rapid colonization (e.g. grazed patches, faeces, surfaces opened by comminution). Some of the fungal species regularly found associated with the body parts of the fauna, are also highly preferred faunal food sources (e.g. *Cladosporium* spp.), consequently there may be a mutualistic relationship between animal and fungus in this case. Swift (1976) felt that fungi such as mucoraceous species could effectively avoid competition by having a life cycle based on a repeated pattern of short time spans between spore and spore. He postulated that such organisms would benefit from the constant opening of 'pioneer' microhabitats by the soil animals.

Organisms capable of colonizing freshly opened resource areas would presum-

ably be those with the highest inoculum potential on or in the vicinity of the soil animal, e.g. the bacteria and fungi mentioned previously. Presumably both groups of micro-organisms would rapidly exploit new resources, with the bacteria dominating if extensive water films are present. If microbial propagules associated with soil fauna are predominantly those which exhibit rapid germination and growth, this would provide a mechanism by which nutrients made available by the fauna could be quickly immobilized rather than be lost through leaching. Caution should be exercised when assuming that it is only the heavy sporulating fungi which are most frequently transported by soil fauna because much of the available data is based on isolations made on synthetic media which select for fast growing, heavily sporulating fungi (i.e. *r*-selected organisms). It should be kept in mind that many of the mycorrhizal fungi, due to their specific growth requirements, cannot be isolated, hence the role of the fauna in their dispersal may be considerably underestimated. This applies particularly to the vesicular-arbuscular mycorrhizal fungi.

Soil invertebrates may alter fungal community structure by increasing the heterogeneity of microhabitats for colonization by the exposure of previously uncolonized microhabitats and the production of faecal pellets. It is frequently overlooked that the soil fauna donate substantial amounts of chitin and other substrates to litter-soil systems through exuviae and dead tissues, thus increasing resource heterogeneity. Cornaby (1973, in Seastedt & Tate 1981) estimated that there were approximately 984 mg m^{-2} of arthropod exoskeletons in a southern Appalachian pine ecosystem, but since this was based on hand sorting of litter it was believed to be an underestimate. Most of the data on fungi associated with animal debris have come from incidental observations, e.g. Warcup (1965) observed that the fungi included animal parasites (*Conidiobolus*, *Entomophthora*, and *Beauveria*) and many saprophytes (*Absidia*, *Cunninghamella*, *Mucor*, *Penicillium*, *Aspergillus*). Among fungi commonly transmitted by micro-arthropods are *Mortierella* spp., many of which are highly chitinolytic, and their frequent presence on animals may be one mechanism by which they can successfully compete for chitin substrates when the animal moults or dies. A similar suggestion has been made by Pherson & Beattie (1979). *Mortierella* spp. may also be instrumental in the turnover of chitin in dead fungal mycelium and may aid in the decay of hyphal fragments in faecal pellets. Insect parasites such as *Beauveria bassiana* are also frequently isolated from the exterior parts of soil fauna and if their inoculum potential is high enough they may successfully infect the animal. Thus, the distribution of fungi such as these within the soil profile is determined by the distribution of their hosts.

Through their dispersal activities, soil animals may affect fungal successional sequences on both roots and decaying litter. Mixing of microbial inoculum may ensure that species found in later stages of succession are redistributed to microhabitats in earlier stages of decay.

Members of the soil fauna move up and down the litter profile in response to changes in moisture conditions (Springett, Brittain & Springett 1970; Metz 1971; Whitford *et al.* 1981; Hassall, Visser & Parkinson 1983). Thus, they may introduce

late successional organisms into areas where competition by indigenous mycoflora has been reduced by microclimatic effects (e.g. prolonged drought in the L layer) or where such a mycoflora has not yet become established. In this way the microbial successional sequence can be advanced and decay rates altered. Similarly the colonization of new short conifer roots may be affected by fungal inoculum introduced by micro-arthropods which previously had been in contact with the fruit-bodies of potential fungal symbionts.

The number of species within fungal communities may be increased as a result of faunal grazing and dispersal activities depending on the grazing behaviour of the animal and the colonizing ability of the organism being grazed. Patchy grazing of a preferred fungus by soil animals could reduce the inoculum potential and hence colonizing ability of the fungus long enough to allow species dispersed by the grazer to colonize the grazed patch. This could result in a short-term increase in species number. If the growth rate of a preferred fungus allows it to tolerate grazing without detrimental effects to its colonizing ability (and, perhaps, even being stimulated due to relief of biostasis), then the dispersed fungi may have little chance of establishing themselves. Therefore, grazing pressure and the competitive ability and growth rate of a preferred food source will determine if species number is altered as a result of establishment of disseminated propagules. Species number may also be increased as a result of comminution and dispersal if the transported propagules are able to colonize newly opened microhabitats. Consequently, it is possible that the comminution, grazing and dispersal activities of the soil-dwelling fauna results in more dynamic microbial communities whose composition is constantly varied in both space and time.

CONCLUSIONS

It is clear from the body of data assembled to date that there are a variety of mechanisms by which soil fauna can influence microbial communities. Comminution and channelling may reduce fungal species richness and divert fungal successional patterns on decaying plant residues. This appears to be a result of the sensitivity of specific fungi to destruction of their thallus and microhabitat, thereby giving a competitive advantage to fast-growing, short life-cycle species commonly associated with the invertebrate body (i.e. bacteria, *Mortierella* spp., *Penicillium* spp.). Grazing by the mesofauna on selected fungi (which may occur during periods of high fungal activity or in systems where hyphal density is high) may have a significant effect on fungal distribution patterns as exemplified by the field studies of Newell (1984a,b), or may deleteriously affect plant growth by reducing the effectiveness of the mycorrhizal symbiosis (Warnock *et al.* 1982). The degree of impact of the fauna on their microbial food sources is probably dependent not only on the grazing pressure of the invertebrate (Hanlon & Anderson 1979), but also on the growth rate of the organism being grazed. More studies are needed to determine if the sensitivity of various micro-organisms (particularly fungi) to a range of grazing pressures is related to the growth rate of the micro-organisms.

Perhaps the most important function of the soil invertebrates is that of dispersal of microbial propagules. It is now well established that soil fauna have associated with them a wide variety of organisms; however, the success of these organisms in establishing themselves in microhabitats differing from those they originally occupied remains undetermined.

Much of the research elucidating the relationship between fauna and the microflora has been restricted to laboratory experiments where extended confinement of experimental animals under optimum temperature and moisture conditions can result in observations which bear little relevance to the field situation. Microcosm studies should be substantiated by field research if we are to gain a more thorough understanding of how fauna affect microbial communities in the presence of varying abiotic factors.

Numerous studies have been performed dealing with the distribution of micro-organisms such as fungi on decaying litter, soil and plant roots, and many inferences have been made regarding the impact of the soil fauna on these distributions. It is only in the last decade that attempts have been made to unravel some of the complex interactions occurring between the wide variety of soil fauna and microflora in the below-ground system. A more precise view of the faunal impact on micro-organisms will depend on separating the effects of the soil fauna from the effects of other factors. This formidable task will demand the combined expertise of soil zoologists and microbiologists.

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